

## Temporal album

### Article (Unspecified)

Vasilaki, E., Feng, J. and Buxton, Hilary (2003) Temporal album. IEEE Transactions on Neural Networks, 14 (2). pp. 439-443. ISSN 1045-9227

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# Temporal Album

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**Abstract**—Transient synchronization has been used as a mechanism of recognizing auditory patterns using integrate-and-fire (IF)-neural networks. We first extend the mechanism to vision tasks and investigate the role of spike dependent learning. We show that such a temporal Hebbian learning rule significantly improves accuracy of detection. Second, we demonstrate how multiple patterns can be identified by a single pattern selective neuron and how a temporal album can be constructed. This principle may lead to multi-dimensional memories, where the capacity per neuron is considerably increased with accurate detection of spike synchronization.

**Index Terms**—IF-model, transient synchrony, Hebbian learning rule, detection of spike synchronization, temporal vision.

## I. INTRODUCTION

HOW is time represented and processed in the brain? This question is currently asked by many researchers in neuroscience [1], [2], [3]. For example, in barn owls, we know that time difference is used to compute the location of an object [4]. In our visual and sensory motor systems, it is claimed that reaction time is about 200 ms, and so back-propagation of signals or feedback control is almost impossible [5], [6]. Even a relatively fast spinal feedback loop requires about 40 ms time delays, which is too large in comparison to the 200 ms. Since time delay occupies a large proportion of the reaction time, fast and smooth movements cannot be executed by using only feedback control (see [6], p. 719, Fig 1). To reveal the functional role of time in signal processing, Hopfield and Brody proposed an artificial organism, “mus silicium”, in the form of a quiz/solution for the scientific community [7], [8]. The winning solution was presented in [9]. Mus silicium consists of a simple IF network and is able to recognize 10 monosyllables using the principle of transient synchronization.

The system proposed has four stages. At the first stage, voice samples undergo spectrographic analysis by Fourier Transformation. This transform gives spatiotemporal patterns of events by detecting onsets, offsets and peaks of power within different bands. At the second stage, there are a number of linear output neurons called A-layer with different decay rates, each of which is associated with a particular event. Due to different decay rates, the outputs of certain neurons will coincide for a particular input pattern. This output feeds a group of weakly connected IF neurons at the third stage, which will start firing in synchrony when the input currents coincide.

Manuscript received September 19, 2002. This work was supported in part by the foundation General Michael Arnaoutis, EPSRC(GR/R54569), Wellcome Trust and Royal Society. E.Vassilakis is corresponding author, at the School of Cognitive and Computing Sciences (COGS), University of Sussex, Falmer, Brighton, East Sussex, BN1 9QH, UK (phone: +44 1273 873073; fax: +44 1273 671320; e-mail: helenv@cogs.sussex.ac.uk). J. Feng and H. Buxton are at the School of Cognitive and Computing Sciences (COGS), University of Sussex, UK.

Then at the fourth level, there is a detection neuron for each pattern stored, which receives input from the previous layer and fires when the sub-group of neurons that is associated with it synchronizes.

The two key issues we consider here are:

- Whether the same principle of transient synchrony applied to sound can be applied to vision tasks. If so, transient synchrony would become a universal principle for recognizing audiovisual patterns and open interesting questions both in neuroscience itself and in applications. For a recent review on how the olfactory system uses time information, we refer the reader to [10].
- Whether the pattern selectivity can be improved by learning and exploited to increase the capacity of the network. Accuracy in coincidence detection determines how many different patterns can be detected. The temporal selectivity may lead to multi-dimensional memories, where patterns are represented not only by different neurons but also by the firing time of one particular neuron.

In the current paper, we answer these two questions. We first generalize the mechanism [7], [8], [9] to detect vision inputs, based upon well known psychological results. We then consider the problem of detection accuracy of the network. In our simulations, we randomly set weak connections, both excitatory and inhibitory, and compare the results with simulations where a temporal Hebbian learning rule was applied. Results demonstrate an average 50% increase in accuracy of detection in the latter case. [Also simulations demonstrate that the time window of the detection neuron is affected by the coincidence point of neurons in the W-layer (Fig. 1). This effect of temporal specificity offers the ability to distinguish between signals that coincide at the same current level, but at different times. ]

In addition, we are offering a greatly enhanced method for going from biology to engineering. We need not only to demonstrate the principles of temporal encoding in signal processing but also how to learn and refine networks for particular applications such as the temporal album for face recognition developed here. Although previous authors, e.g. [11], have engineered solutions exploiting temporal encoding for particular applications, here we use learning rules from biology to improve on the range and flexibility in the set of potential tasks that could be tackled.

## II. TIME DELAY IN VISION SYSTEMS

There is evidence that the brain responds differentially to various frequencies, in particular, it responds faster to low frequencies than high frequencies [12]. Within a natural image, there are a number of spatial frequencies. Gabor wavelet analysis can reveal this by using appropriate localized receptive fields.

Daugman [13] has shown that 2D Gabor elementary functions are fundamental in the visual processing systems of several mammalian species.

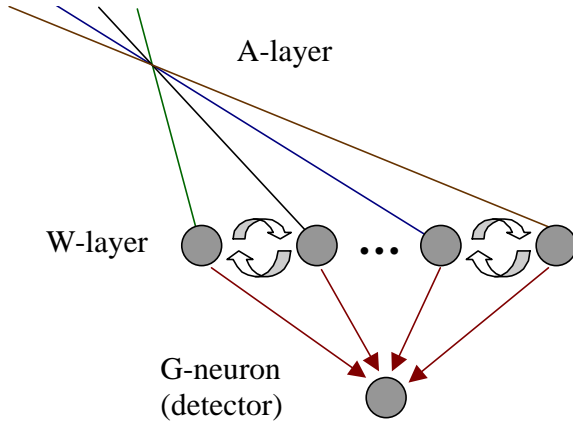


Fig. 1. IF network used in simulations. A-layer is the input, W-layer (126 neurons) is the synchronization level and G-neuron is a detector unit. Each neuron in A-layer is connected to one neuron at W-layer and all neurons in W-layer are connected to G-neuron via a single weight. Neurons in W-layer are set as either excitatory or inhibitory, with equal probability, and are connected via weak all-to-all weights within the layer.

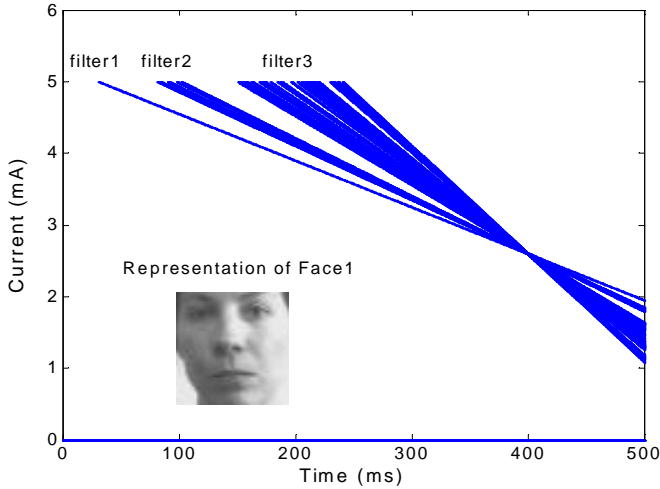


Fig. 2. Example of representation of a face with the output of neurons associated with the coefficients of the three Gabor filters.

Previous research [14] has shown that 126 coefficients, produced using 3 different Gabor filters, are sufficient to distinguish faces using the well-known Radial Basis Function (RBF) network. The network used is a two-layer, hybrid learning network, with a supervised layer from the hidden output units, and an unsupervised layer, from the input to the hidden units, where individual Gaussian functions for each hidden unit simulate the effect of overlapping and locally tuned receptive fields.

Gabor filters, reviewed in [15], have a real (cosine) component,  $C$ , and an imaginary (sine) component,  $S$ :

$$C(x, y) = N \exp\left(-\frac{x^2 + y^2}{2\sigma^2}\right) \cdot \cos(x'\omega) \quad (1)$$

$$S(x, y) = N \exp\left(-\frac{x^2 + y^2}{2\sigma^2}\right) \cdot \sin(x'\omega) \quad (2)$$

where  $x' = x \cos(\phi) + y \sin(\phi)$ ,  $N$  is a real normalization constant and  $\omega = 2\pi/p$ .  $p$  is the period of the harmonic component,  $\phi$  the mask orientation and  $\sigma$  the width, based on  $p$ :  $\sigma = p/2\sqrt{2}$ .

Here we use a similar approach to reveal the coefficients that are correlated with the spatial frequency of the image as in Fig. 2. To reduce the numbers of coefficients calculated for each image, we used a sparse sampling scheme. We use 3 orientations (0, 60, 120 degrees), 3 scales (filter1, 2 and 3), square matrix and minimum overlapping. Using the largest filter (filter1), of the same dimensions as the image, we derive 6 coefficients that correspond to low frequencies. The second (filter2), which is four times smaller, is related to medium frequencies and results in another 24 coefficients. The last (filter3), sixteen times smaller, is associated with the highest frequencies and has 96 coefficients. Therefore, the image can be represented by a total of 126 coefficients. The coefficients produced have negative and positive values and are converted to binary values using a threshold function [14].

An example of a face image and the corresponding coefficients are presented in Fig. 2. Each of these coefficients in their binary form represents an event associated with the image. The neurons respond to these with different delays, due to the precedence of various frequencies and orientations as above. Lower frequencies will cause a faster response than higher frequencies. Hence there are gaps of around tens of ms between filter1 and filter2, and filter2 and filter3 (see [12] p.403 Fig. 28.5). A small delay in response is randomly inserted among the coefficients of the same filter. A large group of analog output neurons are associated with these events and, similar to the audio case [7], [8], the neuronal output coincides at a particular point. Thus, the transient synchrony principle can be applied to visual inputs.

The design of a system that makes use of this principle would be more effective if an appropriate function was automatically chosen for each image, via the Gabor coefficients, to map onto a particular point in Fig. 2. At the moment we are working toward this; the paper explores the benefits of learning in transient synchrony and presents the network architecture as well as simulated results.

### III. NETWORK DESCRIPTION

In the following section, the neural network used in simulations is described in detail. We will briefly discuss the IF model and its parameters (also reviewed by [16], [17]) and explain how such neurons are connected to compose the whole network.

#### A. Neuron Model

Each neuron in the system is modeled according the well known IF model. Let us assume that  $V(t)$  is the membrane potential of a neuron. The equation:

$$\frac{dV(t)}{dt} = -\frac{V(t)}{RC} + I^s(t) \quad (3)$$

describes the dynamics of the leaky integrate-and-fire unit.  $I^s(t)$  is the synaptic input and the  $R, C$  parameters are characteristics of the electrical circuit that models the neuron behavior. The resting potential of the neuron membrane is set to zero. In the simulations we used values  $R = 20$  mOhm and  $C = 1$  mF. As soon as  $V(t)$  reaches a predefined value (threshold), in this case 20 mV, the neuron emits a spike, which is modeled as a delta function. Having sent a spike, the neuron's voltage becomes zero, and retains this value during a refractory period of 10 ms. During this period, the neuron simply ignores any input.

### B. Network Structure

A hundred IF neurons, all-to-all weakly connected, compose the neural sub-network (W-layer) that performs the main part of the recognition task. By weakly connected, we mean that synaptic weights are relatively small in comparison to input signals. Each of these neurons receives an input current (synaptic input), which is comprised of the linear output of one of neurons in the A-layer plus the interaction of the neurons in the W-layer. The synaptic input  $I^s$  for the  $i$ th neuron in the W-layer is of the form:

$$I^s(t) = I_i(t) + \sum_j \sum_{t_{j,k} < t} w_{i,j} \cdot \delta(t - t_{j,k}) \quad (4)$$

where  $I_i$  is the output of the A-layer connected to the  $i$ th neuron,  $w_{i,j}$  is the weight from neuron  $j$  to neuron  $i$  and  $t_{j,k}$ ,  $k = 1, 2, \dots$ , are the times that neuron  $j$  fires.

The output of the neurons in the W-layer becomes input to a detection unit (G-neuron), which decides when these inputs are in synchrony. The detector is another IF-neuron with the same properties as the neurons in the W-layer. This detector is connected to all other W neurons with the same weight  $w$ , which is chosen for each simulation to minimize the number of spikes, ideally to have exactly one spike. If many spikes are generated by the detector, we use only the first one. The network is shown in Fig. 1.

Neurons in the W-layer are randomly set as inhibitory or excitatory connections, with equal probability. Initially, all excitatory weights are set equally strong (0.15) and all inhibitory weights are also equally strong (-0.05). Each W neuron receives an analog input from the previous level, shown in Fig. 1, as well as spikes from all connected neurons. The strength of these connections has an important role in neuron synchronization under a common signal. W connections, in comparison to the input signal, have to be weak; otherwise the system fails to synchronize properly [18], [19]. Strong connections will result in synchrony of neuron firing regardless of their input signal.

## IV. RESULTS

Here the results of the simulations are presented and analyzed. Simulations have been carried out using this type of network with and without the temporal Hebbian learning rule. A comparison of the two cases emphasizes the advantages of the learning process.

For both cases, the decision about which neurons are excitatory induces randomness in the results. Apparently there

are better or worse initial configurations of the weight matrix, which leads to the standard deviation in the simulation results.

In the learning process, we applied a temporal Hebbian rule as in [22], [23], where the weights were restricted in the range  $[-2, 2]$ :

$$w_{i,j}(t+1) = w_{i,j} + L(w_{i,j}(t)) \quad (5)$$

where for  $x \leq u$ ,

$$L(x) = n \cdot \exp\left(\frac{h(x)}{t_1}\right) \cdot \left(1 - h(x) \left(2 \frac{t_1 + t_2}{t_1 \cdot t_2} - \frac{t_0 + t_1}{t_0 \cdot t_1}\right)\right) \quad (6)$$

and for  $x > u$ :

$$L(x) = 2n \cdot \exp\left(\frac{-h(x)}{t_2}\right) - n \cdot \exp\left(\frac{-h(x)}{t_0}\right) \quad (7)$$

with  $h(x) = x/x_0$ ,  $u = -0.005$ ,  $t_0 = 0.025$ ,  $t_1 = 0.15$ ,  $t_2 = 0.25$ ,  $x_0 = 25$  and  $n = 2/30$ , is the function shown in Fig. 3.

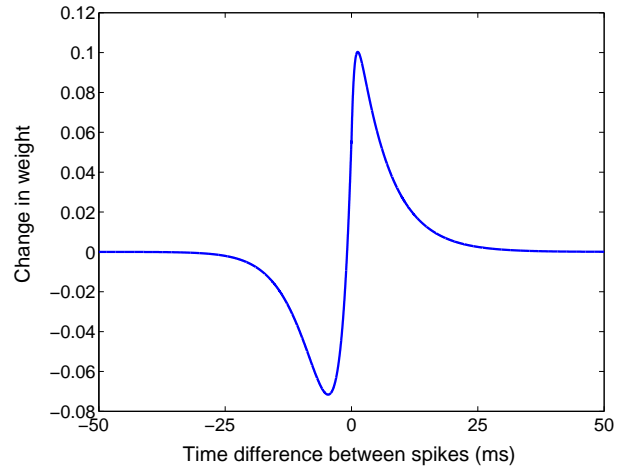


Fig. 3. Hebbian rule applied to the connections of the network.

The ability of temporally asymmetric Hebbian learning to produce predictive coding is a well-known result [26], [27]. We chose this particular type of learning rule mainly because it fits biological data ([24], [25]). However similar results may be achieved by using other learning rules such as the  $\alpha$ -function. It might be worthwhile to point out that we apply the learning rule “on line”, i.e. while processing each input data. Therefore there is no training face in the network and for each input, the network connections are re-initialized.

The error in the simulations is measured as the absolute difference between the synchronization point (the point where the detection neuron first fires) and the coincidence point (the point where the input currents actually meet).

### A. No Learning Process

Extensive simulations have been carried out, in an attempt to assess the accuracy of the model in detecting the actual time

where the network input coincides. A small sample (15 weight sets) is presented in Fig. 4, created with the procedure described in III-B.

The average error for the network with a coincident point at 400 ms is 50 ms and the standard deviation of the distribution 53 ms (see Fig. 5a). These results have been calculated over 200 samples, which is a reasonable sized dataset as increasing samples to 300 changed the values less than 5%. are particularly poor, when used to identify the synchronization point, therefore cannot possibly be used to detect the actual synchronization time.

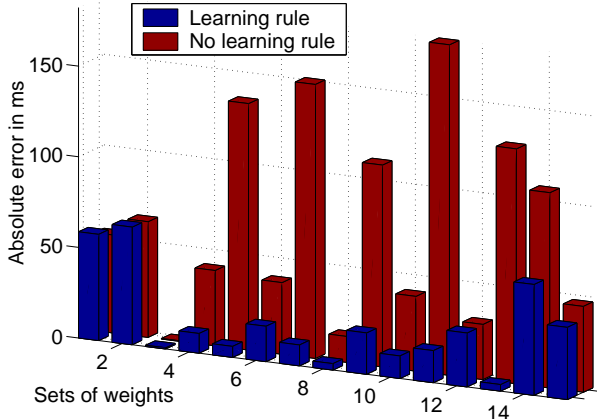


Fig. 4. Hebbian rule applied to the connections of the network.

### B. Learning Process

To have a straightforward comparison between this and the previous case, the 100 initial weight matrices used in the learning examples were identical with those in the non-learning case. The results for applying the learning rule to excitatory weights only, for a coincidence point at 400 ms and for a small sample of 15 initial weight matrices, are plotted in Fig. 4 (learning rule). In the 15 trials, there are just two cases with relatively high error, where one can assume that the initial conditions were so poor that the application of the learning rule was not able to decrease the error enough. For the coincidence point at 400ms, the average error over 200 samples is 26ms and the standard deviation 22 ms (see Fig. 5b). Here the application of the Hebbian learning rule clearly improves the detection of the synchronization by an average value of 50% (see Fig. 5c).

It is noticeable that, while average values of excitatory weights before and after the learning rule are 0.15 and 0.19 respectively, an increment of 2.5%, the maximum weight value significantly increases after applying the learning rule from 0.15 to 1, an increment of 900%.

Absolute numbers for error and standard deviation change as the synchronization point moves along the time scale, but the relative advantage of applying the learning rule remains. Figure 5 shows an increase of the relative error as a function of the coincidence point.

The advantage of applying the learning rule remains at all the timescales examined, though error is worse as the coincidence

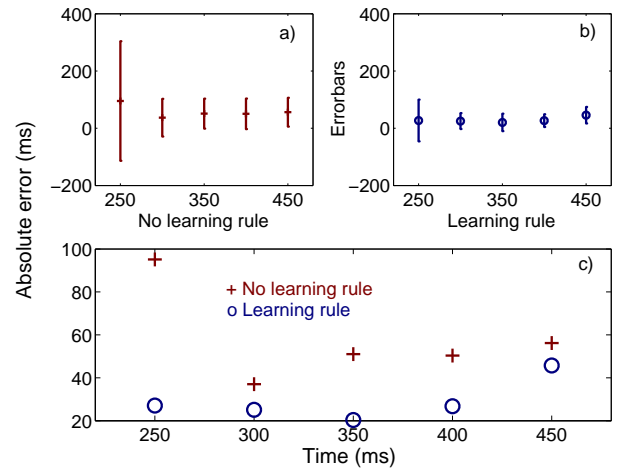


Fig. 5. Comparison of the error distribution between learning and no learning cases versus the time of the coincidence point. a) Mean and standard deviation for

point moves further along the time axes. This can be explained since leaving the coincidence point later in time will result in current values close to each other at an earlier time. This may be detected by the neuron as false common input, and thus the error in detection increases.

### V. DISCUSSION ON THE LEARNING RULE EFFECTS

The comparison of the results in IV-A and IV-B shows that there is a significant improvement when applying the Hebbian learning rule to the IF-network (Fig. 5). An explanation follows: Let us assume that neurons one and two are connected and that neuron one happens to fire before neuron two. Each time that neuron one fires, the potential of neuron two will be increased by an amount determined by the strength of their connection. The first neuron thus increases the amount of charge that the second neuron receives. This additional charge helps the two neurons to synchronize; otherwise the initial time difference between their spikes would be maintained under common input. The fact that the first neuron fires before the second neuron causes the weight to be increased according to the temporal Hebbian learning rule. This would lead to a faster synchronization in comparison to the case where the weight remains constant, and this is verified by the experimental results. Applying the learning rule can be significant in the case when we want the detection neuron to be able to recognize more than one pattern. The accuracy of the detection is critical in order to answer the question of how many patterns a single neuron is able to recognize.

Hopfield and Brody have proposed a method to transform audio signals into spatiotemporal events [7], [8]. A group of IF-neurons associated with the spatiotemporal events leads to analog outputs that coincide at a single point. In this way, a pattern is represented by a single point in the current versus time graph (Fig. 2). Assuming that this representation is unique, in theory infinite patterns can be stored in a single sub-network as described in III-B, since there are infinite points in the 2D space of current level versus time. Recognition of the pattern becomes as simple as the detection of spike synchronization in a group

of neurons. In practice, the number of patterns that a group of neurons can recognize using transient synchrony depends on how well the procedure that transforms the image into a point in the 2D space works, and how accurately the time that currents coincide can be detected.

The application of a Hebbian learning rule to the model can improve the accuracy in timing detection, as shown by the statistical results presented here. Such an improvement results in an increase of the number of patterns that a single neuron can identify. The pattern is not only associated with the spike of the detection neuron but also with the time that such a spike happens. According to the statistics shown in Fig. 5c, there is an average 50% improvement, when the Hebbian learning rule applies. Additionally (see Fig. 5a,b) the application of the Hebbian learning rule reduces the standard deviation of the error in all cases presented here, a fact that enhances the benefits of the Hebbian learning rule. An interesting phenomenon we observe from Fig. 5 is that the standard deviation of the absolute error is extremely high. One might want to know whether this is an intrinsic property of the network of IF model. In fact, it is well known in the literature that the variability of efferent spike trains of the IF model could be very high, if the IF model receives an exactly balanced input[20]. Define the coefficient of variations (CV) of interspike intervals (ISIs) as the mean divided by standard deviation, we then have

$$CV \sim 1$$

In words, the standard deviation of ISIs is proportional to its mean. Results presented in Fig. 5 fits well with the aforementioned conclusions in the literature. Furthermore, we have pointed out in [21] that to generate a high CV ( $CV \sim 1$ ), the exactly balanced input condition can be relaxed. In conclusion, the observed high standard deviation of interspike intervals in Fig. 5 is an intrinsic property of the IF neuron.

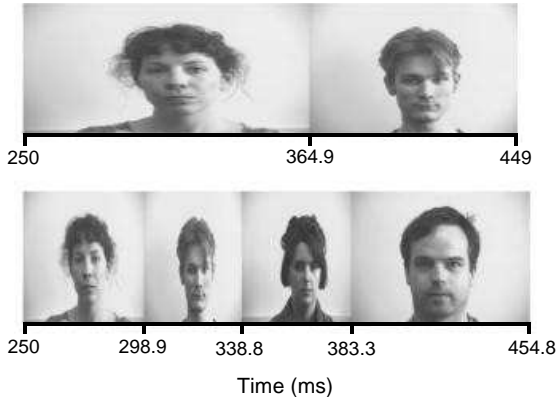


Fig. 6. Temporal album constructed according to Fig. 5. The upper panel corresponds to the case of no learning and the bottom panel to the case with learning.

## VI. CONSTRUCTION OF TEMPORAL ALBUM

Now we are in a position to explicitly spell out the functional implications of our results, i.e. the impact of learning rule on vision recognition tasks. Assume that input currents coincide at

time  $t_0$ . Let us denote the functions fitted according to Fig. 5 as  $f(t)$  (without learning) and  $g(t)$  (with learning). It is found that

$$f(t) = 0.0018 \cdot t^2 - 1.44 \cdot t + 330 \quad (8)$$

and

$$g(t) = 0.0018 \cdot t^2 - 1.17 \cdot t + 210 \quad (9)$$

Therefore, one face can be recognized within the time window  $[t_0 - f(t_0), t_0 + f(t_0)]$  in a non-plastic network. For example, in Fig. 6, upper panel, for the lady face (Face1 in Figure 2) we have  $t_0 = 309.7$  and  $f(t_0) = 59.7$ . Therefore, for Face1, the system can learn so that the currents corresponding to filter1, filter2 and filter 3 meet at 309.7 msec. With appropriate weights and within time window  $[t_0 - f(t_0), t_0 + f(t_0)] = [250, 364.9]$ , the G-neuron will emit a spike if Face1 is presented to the system. For the gentleman's face in Fig. 6, we term it Face2. Its coincidence point is at  $t_0 = 406.95$  msec. Within time window  $[364.9, 449]$ , the G-neuron will fire a spike, Face2 is then recognized. Similarly in a plastic network, we have time window  $[t'_0 - g(t'_0), t'_0 + g(t'_0)]$ , where  $t'_0$  is the coincidence point for a face and  $g(t'_0)$  is the error at  $t'_0$ . In Fig. 6, we construct such an album in which each time window is disjoint. This tells us the maximum number of faces the network is able to recognize in the time interval  $[250, 450]$  ms. Fig. 6 is called a *temporal album*. It is illuminating to note that without the learning rule, the network is only able to detect 2 faces within the given time window. With the learning rule, the network with a single detector can then recognize 4 faces, doubling the capacity, a very substantial improvement. Note that we have not taken into account the variance, which is also reduced with the learning rule. Hence with variance, the learning rule can achieve an even greater improvement, in comparison with the case without learning.

We have constructed temporal album, using other face and even voice data as well. Our results tell us that the improvement with learning is always significant.

## VII. CONCLUSION

In this paper we presented a method to apply the principle of transient synchrony to images using an IF network. We also showed that the application of a temporal Hebbian learning rule in the system improves detection accuracy for common input. Based on this principle we constructed a temporal vision album to demonstrate the benefits of this approach.

The learning rule has a direct effect on the capacity of the network's memory and can significantly increase its ability to recognize images. Thus, a whole system can be developed, which transforms image data to a point in the 2D space of input current versus time, for our IF-network. The IF-network is then able to distinguish among different data on the basis of the time that the detection spike appears. This technique leads to improvement of the memory capacity, as demonstrated by the construction of the temporal album, and can be used when either audio or visual signals are processed.



Interestingly, tackling engineering problems with neural networks in the time domain has been long pursued by many researchers (see for example [11], [28]). However, Hopfield and Brody's approach seems interesting and is close to biology.

In the current paper we concentrated on the time domain of neural information processing and only considered the temporal album. Clearly we could construct a spatiotemporal album. In Fig. 2, we construct the temporal album according to different coincidence points in the time domain, but in the spatial (current) domain, the detection of signals is also determined by different input currents. Hence we can construct a complete spatiotemporal album for future publication.

It is not surprising to see that a reasonable learning rule will improve the performance of a network. The significance of our finding here is that the learning rule can enhance the performance within such a short time window, only a few hundred milliseconds as in the range of a biology reaction time [5], [6]. We expect our results here will be interesting to both neuroscientists and signal processing engineers. Finally we point out that there is mounting experimental evidence to support the importance of information processing in time in the brain (see for example [29], [30]), which is different from the traditional approach of the neural network community, where usually the mean firing rate is used to process information.

#### ACKNOWLEDGMENT

We are grateful to two referees for their constructive comments on an early version of the paper, and thank A. Jonathan Howell for providing the image database, Gabor filters and coefficients. Image database and 2-D Gabor filter masks are public available from: <http://www.cogs.susx.ac.uk/users/jonh/>.

#### REFERENCES

- [1] W. Bialek, F. Rieke, R. R. de Ruyter van Steveninck and D. Warland, "Reading a neural code", *Science*, vol. 252, pp. 1854–1857, 1991.
- [2] J. J. Hopfield, "Pattern-recognition computation using action-potential timing for stimulus representation", *Nature*, vol. 376, pp. 33–36, 1995.
- [3] Z. F. Mainen and T. J. Sejnowski, "Reliability of spike timing in neocortical neurons", *Science*, vol. 268, pp. 1503–1506, 1995.
- [4] W. Gerstner, R. Kempter, J. L. Van Hemmen, Hermann Wagner, "A neuronal learning rule for sub-milliseconds temporal coding", *Nature*, vol. 384, pp. 76–78, 1996.
- [5] S. Thorpe, D. Fize, C. Marlot, "Speed of processing in the human visual system", *Nature*, vol. 381, no. 6582, pp. 520–522, 1996.
- [6] M. Kawato, "Internal models for motor control and trajectory planning", *Curr. Opin. Neurobiol.*, vol. 9, no 6, pp. 718–727, 1999.
- [7] J. J. Hopfield and C. D. Brody, "What is a moment? 'Cortical' sensory integration over a brief interval", *PNAS*, vol. 97, no 25, pp. 13919–13924, 2000.
- [8] J. J. Hopfield and C. D. Brody, "What is a moment? Transient synchrony as a collective mechanism for spatiotemporal integration", *PNAS*, vol. 98, no 3, pp. 1282–1287, 2001.
- [9] S. A. Wills, "Recognizing speech with biologically plausible processors", Hamilton prize 2001 submission, [Online]. Available: <http://www.inference.phy.cam.ac.uk/saw27/hamilton.pdf>
- [10] R. W. Feiedrich, and M. Stopfer, "Recent dynamics in olfactory population coding", *Curr. Opin. Neurobiol.*, vol. 11, pp. 468–474, 2001.
- [11] X. Liu, D. L. Wang "Range image segmentation using a relaxation oscillator network", *IEEE Trans. Neural Networks*, vol. 10, no 3, pp. 564–573, 1999.
- [12] M. McCarthy, "Physiological studies of face processing in humans", *The New Cognitive Neuroscience*, second edition, M. S. Gazzaniga ed., Mit Press, 2000, pp. 393–409.
- [13] J. G. Daugman, "Two-dimensional spectral analysis of cortical receptive field profiles", *Vision Research*, vol. 20, pp. 847–856, 1980.
- [14] A. J. Howell and H. Buxton, "Invariance in radial base function neural networks in human face classification", *Neural Processing Letters*, vol. 2, no 3, pp. 26–30, 1995.
- [15] A. J. Howell, "Automatic Face Recognition using Radial Function Networks", *PhD thesis*, 1997.
- [16] J. Feng, "Is the integrate and fire model good enough? - a review", *Neural Networks*, vol. 14, pp. 955–975, 2001.
- [17] C. Koch, *Biophysics of Computation. Information Processing in single neurons*, New York: Oxford, 1999, Ch. 14.
- [18] Y. Kuramoto, "Chemical oscillations, waves and turbulence", *Springer*, Berlin, 1984.
- [19] H. Sakaguchi, Y. Kuramoto, "A soluble active rotator model showing phase-transitions via mutual entrainment", *Progr. Theoret. Phys.*, vol. 76, no 3, pp. 576–581, 1986.
- [20] Shadlen M.N., and Newsome W.T.(1994). Noise, neural codes and cortical organization, *Curr. Opin. Neurobiol.* **4**, 569–579.
- [21] Feng J., and Brown D.(1999). Coefficient of variation greater than .5 how and when? *Biol. Cybern.* **80**, 291–297.
- [22] R. Kempter, C. Leibold, H. Wagner and J. L. Van Hemmen "Formation of temporal-feature maps by axonal propagation of synaptic learning", *PNAS*, vol. 98, no 7, pp. 4166–4171, 2001.
- [23] R. Kempter, W. Gerstner and J. L. Van Hemmen "Hebbian learning and spiking neurons", *Phys. Rev. E*, vol. 59, pp. 4498–??, 1999.
- [24] G. Q. Bi and M. M. Poo "Synaptic modifications in Cultured Hippocampal Neurons: Dependence on Spike Timing, Synaptic Strength, and Post-synaptic Cell Type", *J. Neurosci.*, vol. 18, no 24, pp. 10464–10472, 1998.
- [25] L. F. Abbot and Sacha B. Nelson "Synaptic plasticity: taming the beast", *Nature Neurosci.*, vol. 3, pp. 1178–1183, 2000.
- [26] R. P. N. Rao and T. J. Sejnowski "Predictive learning of temporal sequences in recurrent neocortical circuits", *Complexity in biological information processing*, vol. 239, pp. 208–233, Novart. Fnd. Symp., 2001.
- [27] R. P. N. Rao and T. J. Sejnowski "Spike-timing-dependent Hebbian plasticity as temporal difference learning", *Neural comp.*, vol. 13, no. 10, pp 2221–2237, 2001.
- [28] A. Delorme, L. Perrinet, S. J. Thorpe, "Networks of integrate-and-fire neurons using Rank Order Coding B: Spike timing dependent plasticity and emergence of orientation selectivity", *Neurocomputing*, vol. 38, pp. 539–545, 2001.
- [29] T. Sakaba, and E. Neher, "Calmodulin mediates rapid recruitment of fast-releasing synaptic vesicles at a calyz-type synapse", *Neuron*, vol. 32, pp. 1119–1131, 2001.
- [30] M. Migliore, L. Messineo, M. Cardaci and others, "Quantitative modeling of perception and production of time intervals", *J Neurophysiol.*, vol. 86, pp. 2754–2760, 2001.